BODY MOLT OF MALE LONG-TAILED DUCKS IN THE NEAR-SHORE WATERS OF THE NORTH SLOPE, ALASKA

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ABSTRACT.—We examined the timing and intensity of body molt in relation to stage of remige growth for postbreeding adult male Long-tailed Ducks (*Clangula hyemalis*) off the coast of northern Alaska. During this period, remige and rectrix feathers are molted simultaneously with body feathers during the prebasic molt, which results in a period of increased energetic and nutritional demands. We collected birds from late July through mid-August and recorded intensity of molt in eight regions: head and neck, back and rump, greater coverts, lesser coverts, flank and sides, breast, belly, and tail. Using nonlinear regression, we estimated the peak intensity and variation for each region in relation to ninth primary length. We found little evidence of molt in the head and neck region. The greater and lesser coverts, and back and rump reached peak molt intensities earliest and were followed by tail, breast, and belly. Molt intensity in the flank and side region was highly variable and indicated a more prolonged molting pattern in relation to other regions. While body molt occurs simultaneously with wing molt, we found that molt among regions occurred in a staggered pattern. Long-tailed Ducks may employ this staggered molting pattern to minimize the energetic and nutritional requirements of molt. *Received 16 July 2002, accepted 22 February 2003.*

Each year during July and August adult male Long-tailed Ducks (*Clangula hyemalis*) migrate in large numbers to the near-shore waters of the North Slope of Alaska (Johnson and Gazey 1992). The shallow lagoons of the region range from 2–3 m in depth and are protected by barrier islands that shelter the lagoon system from high winds and ice flow. During this period, Long-tailed Ducks undergo the prebasic molt (Humphrey and Parkes 1959).

Whereas the molting regimes of most species of waterfowl consist of one or two molting cycles per year (i.e., pre-alternate and prebasic), Long-tailed Ducks are unique in that they carry out an additional third, supplemental molt (Salomonsen 1949, Humphrey and Parkes 1959, and Palmer 1976). The supplemental molt occurs from approximately September through mid-October, between the prebasic and pre-alternate molts, and involves replacement of the head, neck, and scapular regions (Palmer 1976). Subsequently, pre-alternate molt occurs gradually from some time in September through November or December. This molt involves the replacement of all feathering except the tail, wing, and posterior underparts of the bird (Palmer 1976). Prebasic molt occurs in two periods. During spring (commonly April; Palmer 1976), areas including the head down to the breast and much of the mantle are molted. Prebasic molt resumes in late summer (July) and continues into fall when male Long-tailed Ducks molt the remaining body regions as well as remiges. During this molt Long-tailed Ducks are flightless for approximately 3–4 weeks (Palmer 1976).

Molt can be a useful indicator of the physiological status, habitat requirements, and probable fitness of migratory waterfowl (Lovvorn and Barzen 1988). Understanding the timing of prebasic molt is important since it occurs with the wing molt, a period that leaves waterfowl vulnerable to disturbance and predation. During this period birds may lose as much as 25% of their total body mass (Chilgren 1977, King 1980). Nutrient demands increase for the synthesis of new feathers, increased amino acid metabolism, increased cardiovascular activity, daily protein requirements, increased production of red blood cells, and augmented bone formation (Murphy and King 1992). Birds can cope with the added costs of molt by increasing foraging effort, reducing other nutrient costly activities, catabolizing stored nutrients, or a combination of the three (Ankney 1979, Murphy and King 1982). Catabolized reserves often play an important role in supplying the necessary nutri-

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ents to carry out feather replacement (Hanson 1962, Howell 2002, but see Ankney 1979). Therefore, characterizing the body molt as it relates to remige growth provides a composite view of the timing and intensity of molt that could serve as a potential baseline from which to measure the effects of physiological or environmental pressures on the population. Our primary assumption was that while the precise timing of molt may vary among years and individuals, the relative timing of feather molt is a good indicator of the physiological status and capability of individuals to meet the nutritional demands of the process. Our objective was to describe the timing and intensity of body molt in relation to the stage of remige molt as it occurs in adult male Long-tailed Ducks.

METHODS

We conducted this study at two sites in near-shore waters of the Beaufort Sea on the northern coast of Alaska, Simpson Lagoon (70° 32′ N, 149° 26′ W) and an unnamed lagoon formed by the Maguire Islands and Flaxman Island (70° 12′ N, 146° 19′ W). During the summers of 1999 and 2000 we attempted to obtain comparable samples of birds from each site representing all stages of the wing molt from just following remige loss through feather growth and re-attainment of flight. We obtained specimens by euthanizing birds captured during banding operations or by shooting after significant numbers of flightless birds had been observed in the area in accordance with Auburn Univ. Animal Care and Use Committee guidelines. We shot individuals from flocks after first establishing their inability to fly by observations from blinds or by approaching them with small boats. We selected individuals for euthanasia during banding drives based on the length of the ninth primary in order to ensure broad distribution of molt stages and dates. Specimens then were frozen and transported to Auburn Univ. for laboratory analysis.

We determined stage of wing molt by measuring the length of the ninth primary from the tip of the feather to its insertion on the proximal side of the feather. To measure the intensity of body molt, we assigned feather tracts into eight regions: (1) head and neck (crown, facial, chin/throat, and neck), (2) back and rump (upper and lower back, scapulars, rump), (3) breast (chest), (4) belly; (5) greater coverts, (6) lesser coverts, (7) side (flank and side), and (8) rectrices, based on Billard and Humphrey (1972). We sampled each region four times by estimating the proportion of blood quills and missing feathers along a 2.54-cm dissecting probe inserted between feathers at random locations. We defined a blood quill as any growing feather containing blue color within the shaft or any feather with feather sheath present at or above the skin surface. We categorized molt intensity into five levels based on the estimated portion of blood quills and missing feathers in each sample: 0 (0%), 1 (1–25%), 2 (26–50%), 3 (51–75%), and 4 (>75%) based on Taylor (1995), and recorded the mean score for each region.

Analysis.—We were interested in estimating the intensity and duration of molt for each feather tract with respect to the stage of wing molt. We sought to do so using a model that would adequately describe the distribution of molt intensity scores with respect to remige length using biologically interpretable and estimable parameters. Although linear, polynomial, and other nonlinear models could adequately describe the shape of the sample distribution, they failed to incorporate meaningful information about similar biological phenomena that occur during finite time periods. Thus, we selected a model that would estimate the mean maximum molt intensity, the timing of maximum molt intensity, and variability in molt intensity over time. We used nonlinear regression (Sigmaplot 2001 ver. 7.0; SPSS, Inc. 2001) to fit the Gaussian three-parameter model,

$$y = a \exp\left[-0.5\left(\frac{x - x_0}{b}\right)^2\right],$$

where the estimated parameter a corresponds to the function maxima, b determines the width of the bell curve, x is the independent variable, x_0 is the estimated value of the independent variable at the corresponding function maxima, and y is the dependent variable. Thus, for a given feather tract and individual, y and x are the observed molt score and length of the ninth primary (i.e., molt stage). It follows then that the population parameters estimated for each feather tract are, a = mean
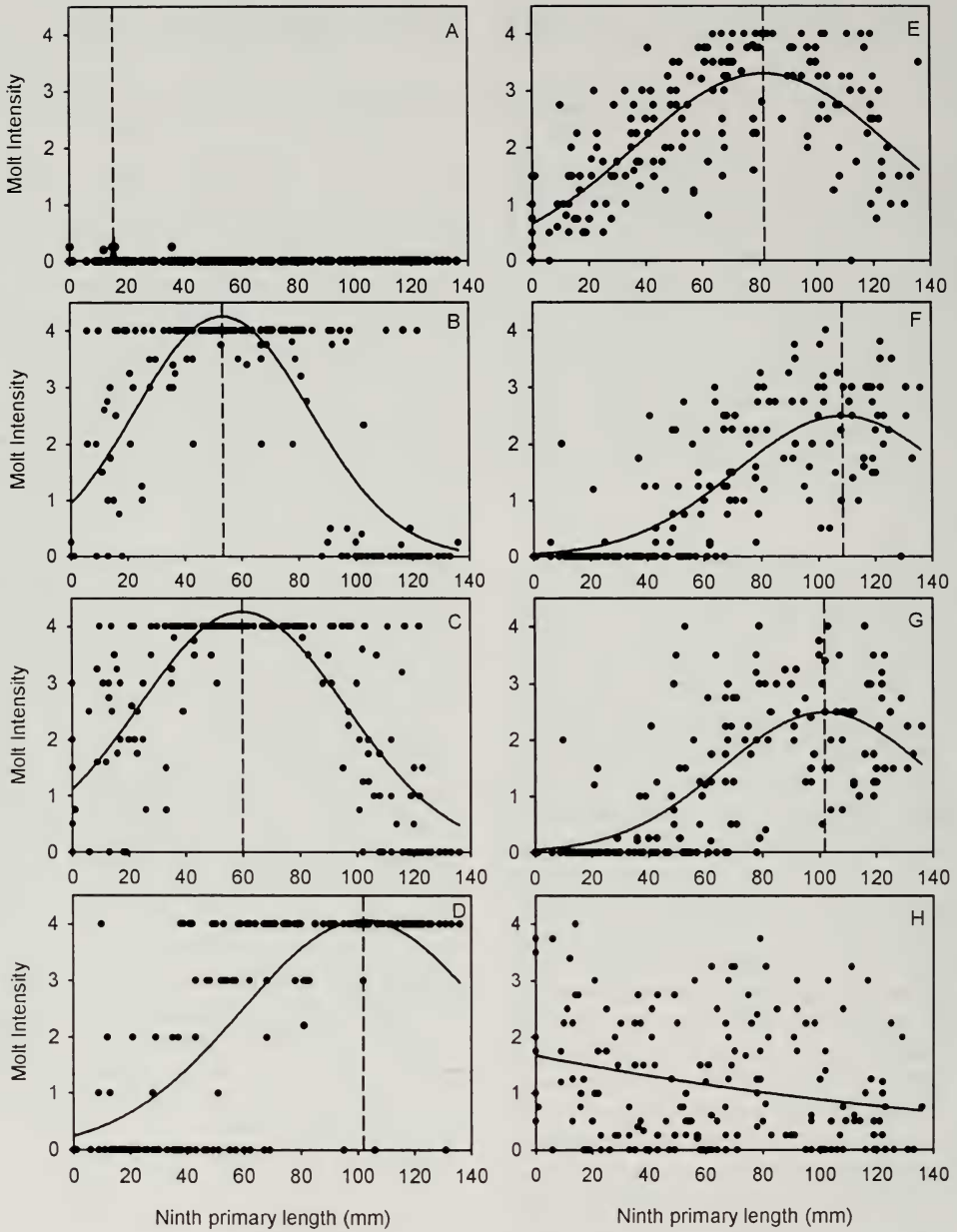
FIG. 1. Distributions of molt intensity scores for adult male Long-tailed Ducks by body region: (A) Head and neck, (B) lesser coverts, (C) greater coverts, (D) tail, (E) back and rump, (F) belly, (G) breast, and (H) flank and side. Score distributions indicate that the timing of molt varied with respect to stage of remige regrowth. Solid lines are mean-fitted distributions, and dotted lines indicate the estimated stage of wing molt (i.e., ninth primary length) corresponding to peak molt intensity.

peak molt intensity, b = variation in molt intensity with respect to molt stage, and x_0 = length of ninth primary at which molt intensity peaks. A high degree of synchrony in molt among individuals resulted in good mod-

el fit as indicated by a large R^2. Large variability in timing of peak molt intensity with respect to molt stage was indicated by a relatively large b. Thus, a small R^2 in concert with a large value for b suggested a low de-

TABLE 1. Intensity of body molt of adult male Long-tailed Ducks using Beaufort Sea lagoons during 1999–2000 varied with respect to the stage of remige molt (length of ninth primary in mm) as indicated by parameter estimates (a, b, x_0) that describe a bell-shaped curves (three-parameter Gaussian models) of molt intensity. Large variation in b and poor model fit (low R^2) suggests that molt on flanks and sides were not synchronous with remige molt.

Region	Maximum intensity (a) Estimate (SE)	Variance in intensity (b) Estimate (SE)	Remige molt stage at peak intensity (x_0) Estimate (SE)	R^2
Head and Neck	0.43 (1.32)	0.38 (0.85)	15.40 (0.47)	0.30
Back and Rump	3.30 (0.10)	45.53 (2.35)	81.59 (1.89)	0.53
Breast	2.49 (0.13)	35.73 (3.40)	101.70 (3.35)	0.52
Flank and Side	8.37 (119.14)	306.61 (1374.08)	−550.31 (5218.59)	0.06
Greater Coverts	4.25 (0.12)	36.44 (1.43)	59.81 (1.30)	0.63
Lesser Coverts	4.25 (0.15)	30.74 (1.36)	53.35 (1.30)	0.65
Tail	4.06 (0.15)	42.84 (3.42)	101.94 (3.49)	0.60
Belly	2.49 (0.11)	37.63 (3.55)	108.52 (3.96)	0.59

gree of synchrony in feather molt at the population level.

RESULTS

We collected specimens ($n = 187$) from 28 July to 14 August 1999, and from 21 July to 10 August in 2000. Long-tailed Ducks molted each body region during our study except head and neck (Fig. 1, Table 1). Although we found evidence of feather regrowth, only six males (3%) showed any degree of molt in the head and neck (Fig. 1A).

During our study, molt intensity achieved the highest levels in the lesser coverts, greater coverts, tail, and back and rump regions. Nonlinear models explained over 60% of the variation in molt scores for lesser and greater coverts. Lesser coverts appeared to reach the highest molt intensity slightly earlier than greater coverts (Fig. 1B and 1C). The back and rump region also reached highest molt intensity when remiges were slightly more than half of their full length (Fig. 1E). Rectrices were the next feathers to reach peak molt intensity (Fig. 1D). Both the lesser and greater coverts appeared to complete the process of molt before remige regrowth was complete, while the back and rump regions were nearly completed during the same time period. Molt of rectrices appeared to have continued into the latter stages of remige regrowth.

Our models explained nearly 60% of the variation in molt scores for the breast region and over 50% for the belly region (Table 1). We found that the breast and belly regions started molt later than the greater and lesser coverts, rectrices, and back and rump regions and attained maximum molt intensity during the latter half of molt. The breast region attained maximum intensity slightly ahead of the belly region (Fig. 1G and 1F). However, the figures indicate that the latter stages of feather growth for the breast and belly regions did not occur within our study period and probably continued until and perhaps beyond full remige regrowth.

Molt in the side and flank region occurred throughout our study (Fig. 1H). Values for molt intensity in this region also were highly variable as indicated by the value of b for this feather tract (Table 1).

DISCUSSION

All feather tracts, except the head and neck and the flank and side regions, increased in molt intensity as wing molt progressed. Our research substantiated Palmer's (1976) characterization that molt occurs in the head and neck region prior to all other feather tracts during the prebasic molt. Molt in the flank and side region appear to be more variable throughout the wing molt and the lack of a discernable peak probably indicates a slower rate of molt in these areas. Both the greater and lesser coverts and the back and rump regions began molting concurrent with the loss of remiges and were regrown by the time remige regrowth was complete.

Long-tailed Ducks may reduce the nutritional demands of molt by staggering the molt of various feather regions over time or by undergoing molt during periods when molt does

not overlap with other nutrient costly activities such as migration (Heitmeyer 1987). Our data indicate that greater and lesser coverts and back and rump regions likely completed molt prior to additional postbreeding movements, which may reduce costs associated with the initiation of the supplemental molt as it begins in September (Palmer 1976). However, King and Murphy (1985) advised that nutritional status should be considered in the context of the life history of a species with regard to nutritional requirements and accessibility, as well as the repertoire of adjustments available to avert or minimize discrepancies between the two. Also, Lovvorn and Barzen (1988) cautioned against the interpretation of molt patterns in terms of staggered costs and found that timing of molt was associated with a photoperiodic response for Canvasbacks (*Aythya valisineria*). Leafloor and Ankney (1991) also suggested that among unsuccessful nesting female Mallards (*Anas platyrhynchos*) social environment appears to influence the timing of molt. For Long-tailed Ducks molting in the cold waters of the Beaufort Sea, a less synchronous pattern of body molt also may lessen the thermal costs associated with reduced insulatory qualities of plumage.

Also, completion of the covert molt prior to full remige regrowth may suggest an adaptive strategy to minimize the flightless period. Many species of waterfowl regain flight before remige regrowth is complete (Hohman et al. 1992). Brown and Saunders (1998) showed that body mass dynamics and wing surface area played a significant role in enabling Blue-winged Teal (*Anas discors*) to re-attain flight capability before remige growth was complete. However, smoothness and shape of the wing also are important in reducing wing drag and maximizing lift (Pennycuick 1989). We suggest that while the overall timing of molt in Long-tailed Ducks may be controlled by ultimate factors such as photoperiod, the sequence of molt among specific feather tracts, specifically the molt of wing coverts, is timed to reduce the period of flightlessness. Further, the staggered timing of molt among feather tracts may serve to spread the nutritional demands of feather growth and reduce the energetic costs associated with thermoregulation in cold water environments.

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